Induced Dominance of Microlaena avenacea (Raoul) Hook. f., in a New Zealand Rain-Forest Area.

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The following paper gives a brief account of a rain-forest in the Thames Sub-district of the South Auckland Botanical District of New Zealand, and describes the development within it of a comparatively stable indigenous induced community dominated by the tall tussocky grass *Microlaena avenacea.* This replacement of one formation (forest) by another (grassland) is the more remarkable in that it has occurred without the intervention of bush-felling or fire, but depends simply upon the progressive action of introduced animals—cattle, pigs and goats.

Practically all the observations on which our conclusions are based were made in the course of a survey of the vegetation of Te Moehau (888m.), the highest and most northerly peak of the broken range that forms the backbone of the narrow Coromandel Peninsula.

In undertaking this survey and throughout its course, as in all our botanical work, we have been indebted, for generous personal help and encouragement, to Dr. L. Cockayne, of Ngaio, Wellington. The special study of the aspect here dealt with was suggested to us by Dr. H. H. Allan, Systematic Botanist at the Plant Research Station, Palmerston North. We particularly thank him for advice on points requiring expert knowledge of agrostology. We should like to express our gratitude also to Mr. G. O. K. Sainsbury, of Wairoa, who checked our identifications of mosses, and to Mr. K. W. Allison, of Rotorua, who kindly named the hepatics.

Except where otherwise mentioned the taxonomic nomenclature used is that of Cheeseman's "Manual of the New Zealand Flora" (2nd Edition) for flowering plants and ferns, and of Dixon's "Studies in the Bryology of New Zealand" for mosses. For hepatics, where there is no general text book available, the authority is quoted with each of the few species mentioned.

Ecological terms are used as defined by Cockayne (1928).

So little has been written concerning *Microlaena avenacea* either in primitive or modified communities, and so little virgin ground remains for investigation, that its original status in New

Zealand forests would be difficult to ascertain. Despite various general records of abundance it appears to be nowhere a common plant in relatively unmodified communities. The succession we describe, therefore, adds to the list given by Cockayne (1928) and supplemented in a recent paper (Cockayne, Simpson and Scott Thomson, 1932), another striking example of the induced dominance of an indigenous species not well represented in the primitive vegetation of this country.

Certainly on Te Moehau there is every indication that *Microlaena* has until recently occurred only very sparingly in areas where it is now almost a pure dominant. Here, where change is still proceeding rapidly, every stage can be seen, and the succession traced with some degree of certainty from the modification of primitive forest to the establishment of a ground-cover of grass, frequently continuous for many hectares at a stretch. Everywhere dead and drying trees or fallen trunks testify to the recent conquest of the forest.

In this remarkable change from forest, the climatic climax for this district, to grassland, man's influence, apart from the initial liberation of cattle, pigs and goats, has been negligible.

Before describing the stages in succession we give a general review of the forest involved, as it appears in least modified portions.

PRIMITIVE FOREST.

The characteristics of this rain-forest before interference are: closed canopy provided by tall trees, an abundance in the middle tiers of saplings, and a wide variety of seedlings, filmy and other ferns and bryophytes amongst the fallen leaves on the humus-rich forest floor. A profusion of epiphytes, both phanerogamic and cryptogamic, of root-climbers and of lianes is typical and physiognomic.

These features are common to several associations, in which also the various stages in succession are quite comparable, although the species-content differs somewhat. The forest is dominated below 510 m. by *Beilschmiedia Tawa* (tawa association), and from 510 m. to 750 m.—the upper limit of *Microlaena*—by *Weinmannia racemosa* (kamahi association), while on certain aspects between 600 m. and 780 m. there occurs a rather peculiar and more restricted rimu-kauri *(Dacrydium cupressinum—Agathis australis)* community to be described in detail in a later paper. Taking a rapid survey of the whole of the forest concerned, the most important members may be listed in the following groups relative to height above ground level.

Estimated frequency is indicated by the following symbols: d., dominant; v.a., very abundant; a., abundant; f., frequent; o., occasional; l., local.

(1) THE CANOPY, which, though always closed, is at lower altitudes rather irregular, the trees varying in height from 9 to

18 metres; but higher up the mountain it presents a more uniform appearance, the trees being about 6 to 9 m. in height and without taller projecting individuals. To this canopy belong *Weinmannia racemosa,* always abundant, and where dominant often with taller crowns projecting conspicuously above the general level; *Quintinia serrata* and *Ixerba brexioides* v.a., somewhat shorter than the dominant in each association, but always forming a considerable portion of the canopy in the area under discussion; *Suttonia salicina,* its importance increasing with altitude and comparable with that of *Quintinia* and *Ixerba* in kamahi forest; *Dacrydium cupressinum* o.–d., big trees projecting above general canopy level in tawa and kamahi associations; *Podocarpus ferrugineus* o., increasing in frequency with altitude; *Agathis australis* l.a.; *Podocarpus Hallii* scattered throughout; *Knightia excelsa* o.–f.; *Carpodetus serratus* o.; *Nothopanax Edgerleyi* o.–l.a., usually beginning life as an epiphyte; *Olearia Cunninghamii* l.a., possibly an indicator of the position of old landslips; *Metrosideros lucida* o., nowhere large; *Laurelia novae-zealandiae,* big trees in steep gullies, otherwise o.

Especially characteristic of the lower slopes are *Beilschmiedia Tawa* dominant up to 510 m. and not occurring above 600 m.; *Melicytus ramiflorus,* as abundant and important in tawa as *Quintinia* and *Ixerba* are higher up; *Hedycarya arborea* o.; *Fuchsia excorticata,* as a big tree almost confined to stream sides, and frequently associated there with *Schefflera digitata.*

Of the species that rarely or never descend into tawa forest the most important are *Phyllocladus glaucus, Nothopanax Colensoi* and *Griselinia littoralis,* as well as *Dracophyllum recurvatum* Col. (see Oliver, 1928) which in kamahi forest forms a real tree with stout trunk, rather erect, very rigid branches and large tufted heads poking through the canopy.

Epiphytes which add to the leafiness of the canopy of tawa forest are *Astelia Solandri,* with which are often associated the filmies *Hymenophyllum flabellatum* and *H. rarum, Asplenium adiantoides, Lycopodium Billardieri* and *Dendrobium Cunninghamii,* as well as the woody epiphytes *Pittosporum Kirkii, P. cornifolium,* and *Senecio Kirkii.* At higher altitudes the tree crowns show typically numbers of leafless branch tips, the smaller ones rather tightly covered with mats of the mosses *Dicnemon calycinum* and *Macromitrium* spp., while those of greater diameter are made to appear even bigger by deep loose cushions of the liverwort *Lepicolea scolopendra* (Hook.) Dum., with which are mixed in varying proportions the filmy *Hymenophyllum multifidum,* and of mosses the tufted *Holomitrium perichaetiale* and the cord-like *Cladomnion ericoides.* The leafy parts of the scrambling climbers *Metrosideros florida* and *Rubus australis* (in the tawa), *Metrosideros albiflora* (in kamahi), and everywhere *Rhipogonum scandens* and *Rubus schmidelioides* add to the density of the forest roof.

(2) MIDDLE LAYERS. Shorter trees and shrubs are mixed with saplings of the taller species. Occurring throughout are

tree-ferns, never very abundant in primitive forest, but represented by *Dicksonia squarrosa* o., *Hemitelia Smithii* o., *Cyathea dealbata* o., and *Cyathea medullaris* o., sometimes very tall in the gullies.

With these are associated *Drimys axillaris* f., *Coprosma grandifolia* always f., sometimes also *C. lucida, Coprosma foetidissima* increasing with altitude, the laxly branched *Alseuosmia macrophylla,* and *Senecio Kirkii* as a sturdy terrestrial shrub.

Rhopalostylis sapida, Nothopanax arboreum and *Geniostoma ligustrifolium,* though characteristic of the lower tawa, barely reach the altitude at which *Microlaena* becomes important. *Dracophyllum latifolium,* a slender tree with widely spread branches topped by sparse tufts of leaves, is abundant in this tier in the tawa forest, but only very rarely does it occur with *D. recurvatum* above the tension belt between kamahi and tawa.

Confined to higher altitudes are *Ascarina lucida,* a compact, bushy little shrub favouring ridges, and the luxuriant purple-stemmed *Nothopanax laetum,* handsomest of all the araliads, and especially characteristic of stream-sides.

Epiphytes are again important on lower trunks of tall trees. Often associated with *Astelia* may be *Tmesipteris tannensis, Lycopodium Billardieri, Asplenium adiantoides, A. flaccidum, Earina mucronata* and *E. autumnalis.* The tufted fern *Polypodium grammitidis* is abundant everywhere. Trunks and low boughs of big trees usually bear some filmy-ferns—*Hymenophyllum sanguinolentum, H. dilatatum, H. demissum, H. flabellatum, H. tunbridgense, H. multifidum* and *Trichomanes reniforme,* are all well represented. Mixed with them are more or less *Lepicolea scolopendra* and *Mastigophora flagellifera* (Nees) Mitt.

Madotheca Stangeri G.L. & N., *Camptochaete arbuscula, Cyrtopus setosus, Weymouthia* spp. seem to be confined to tawa, where they are abundant and always conspicuous. *Hypopterygium concinnum* is also epiphytic towards the bases of trunks.

Of climbers, kiekie *(Freycinetia Banksii)* is abundant throughout and always of physiognomic value. The ratas *(Metrosideros florida, M. scandens, M. albiflora)* mentioned in the description of the canopy, here produce their juvenile leaves, whole trunks frequently being clothed for a metre or more from the ground with their mosaic. Particularly characteristic of the tawa association are three climbing ferns—*Lygodium articulatum, Blechnum filiforme* and *Polypodium diversifolium.*

(3) FLOOR COVER. Abundant throughout are the mosses *Dicranoloma Menziesii, Leucobryum candidum, Ptychomnion aciculare,* with *Camptochaete arbuscula* rather more frequent in tawa. In wetter places *Sciadocladus Menziesii* and the liverworts *Schistochila nobilis* (Hook.) Dum., *Trichocolea australis* St., and species of *Aneura* are noteworthy. Of filmy ferns *Hymenophyllum demissum* is most striking in tawa, while *H. ferrugineum* is occasional towards its upper limits, as also above in the kamahi. *Trichomanes reniforme*

is abundant on old trunks and on wet ground, and the herbaceous creeper *Nertera dichondraefolia* is everywhere in damp places. *Blechnum discolor, B. Fraseri, B. fluviatile,* and *B. lanceolatum* were probably only occasional in the untouched forest, while in the tawa *Asplenium bulbiferum* and *Leptopteris hymenophylloides* would be fairly common. In the kamahi the pale stiff fronds of *Lindsaya cuneata* and the neat little fans of leaves and dainty white flowers of *Libertia pulchella* are a feature of the otherwise dark floor. Here also in the kamahi occur *Blechnum Pattersoni* var. *elongata* and *B. nigrum* in abundance by rocky streams, *Trichomanes Lyallii* o., on damp banks and rocks, and *Trichomanes strictum* characteristically hidden in wet pockets under the elevated much-branched roots.

Microlaena avenacea would not be entitled to mention as one of the important members of this original forest. As far as we can judge it would be represented only by widely separated individuals in the form of slender tufts. It still occurs thus on shaded rocky stream sides.

The important ecological factors are:—

(1) **High and evenly-spread precipitation.** For the sub-district Cockayne (1928) gives 165 cms. annual rainfall, distributed as follows—spring 24.2%, summer 18.2%, autumn 26.8%, winter 30.7%. No local records are available.

(2) **Equable temperature** owing to proximity to the sea, though Cockayne's figures for the sub-district (27°C and –4°C) are certainly exceeded at the highest altitudes.

(3) **High winds** striking from all quarters across long stretches of open sea. Local incidence of wind is affected by the configuration of the steep, narrow gullies.

(4) **A shallow soil,** full of rock fragments and easily bared to the substratum of greywacke or allied rocks.

(5) **Total absence of browsing animals** in the primitive forest.

In the early days of settlement pigs, goats and cattle were introduced and soon became wild on the lower slopes of the mountain. The dates of these introductions cannot be checked, but Adams (1888) mentions that cattle were feeding on native grasses at Torehina, 9 miles south, and Maclaren (1898) speaks of a main ridge track "worn into mud by the wild cattle that abound on Moehau." It would appear then that in no portion have they been effective for more than 50 or 60 years. Wild cattle (of the old stock at least) have been wiped out, but pigs and goats thrive, and in spite of more or less organized killing in recent years they are increasing in numbers and in cumulative effect, tending always to intensify the destructive influence of habitat factors with which the vegetation was formerly in equilibrium.

STAGE I. OF SUCCESSION TO GRASSLAND.

The first obvious effect of these animals is the baring of the forest floor, due to trampling or browsing on seedlings, small plants and low boughs. Pigs root and further disturb the leaf-cover. All this tends to alter the relations with surface-water, which, instead of being held and absorbed, is now free to flow, carrying with it loose leaves, etc., and soon stripping the humus layers below. Retardation of the decay of newly fallen matter follows, with general impoverishment of the soil. Increased wind at ground levels, an inevitable result of the removal of the lower tiers of vegetation, hastens the drying of this bare soil and is, moreover, responsible for the dislodgement of weaker saplings.

At the same time the **continuity of the canopy** is being impaired by falling of trees due to (1) normal over-maturity, (2) premature death following (a) damage to surface roots, (b) ring-barking or wholesale stripping of bark, (c) uprooting of whole trees. This latter is more characteristic of the short superficially rooted trees of higher altitudes.

Landslips, an ever-present danger on these steep slopes, increase in size and number.

The **seed-bed** now provided by the forest-floor may be a bare, impoverished soil, subject to considerable wind action, involving rapid evaporation of water and subsequent dryness, and also exposed to moderately strong light. Though these conditions are impossible for the seedlings of many species which normally form the canopy and upper layers, there are others, comparatively unimportant or even rare in the original forest, which can colonise and hold such a seed-bed. Amongst these the ferns, notorious for their ability to germinate on bare ground, are the most successful, and of these *Hemitelia Smithii* soon springs into prominence. With it are associated in almost equal numbers *Blechnum discolor*, of humbler stature; and in varying quantities according to local conditions *B. procerum* where rather wet, *B. Fraseri* in drier places, and *B. fluviatile* favouring shade. *Drimys axillaris*, *Ascarina lucida*, three species of *Coprosma* (*C. foetidissima*, *C. grandifolia* and *C. lucida*), *Brachyglottis repanda* and *Olearia Cunninghamii* not only survive as small plants from the previous undergrowth, but also regenerate rather freely under the new conditions.

Epiphytes (to some extent) and the scrambling climbers, notably *Freycinetia Banksii* and *Rubus schmidelioides*, thrive and form almost impenetrable masses on ridges where the host trees fall earliest. With this last exception the new undergrowth is not closed, the spaces between the umbrella-shaped *Hemitelia*, the tufted blechnums and the bushy shrubs being taken by a fairly sparse growth of *Carex* spp., *Uncinia australis* (distributed by animals) or slender shade plants of *Microlaena*, their seeds presumably wind-borne from the scattered tufts of the original forest.

The forest has now reached the end of Stage I. of the change.

Position summarised:

(1) CANOPY: Now discontinuous—original dominants still present.

(2) MIDDLE LAYERS: Majority of the smaller trees persisting, *Weinmannia* probably most abundant in both associations. Saplings few, but the tree-fern *Hemitelia Smithii* increasing.

(3) GROUND COVER: As detailed above—rather poor herbaceous content; tufted ferns increasing; *Microlaena* present only as tufts or in small, scattered patches.

STAGE II.

The ferns now grow apace, and if the action of animals were only a temporary set-back, the tree-ferns, of which *Hemitelia Smithii* is by far the most important, would act as nurse plants in the regeneration of something very nearly approaching the original associations in composition and structure. As it is, everywhere, in the abundance of epiphytes and woody hemi-epiphytes which find lodging on *Hemitelia* trunks (where they are for some years out of reach of the destructive influences at work on the forest floor), one sees signs of the struggle made by the forest to re-establish itself. That this is not accomplished is due not only to the continued action of the factors already enumerated, but also to the special attraction these aggressive ferns hold for pigs. *Hemitelia* fronds are chewed by goats, and the trunks even more frequently knocked over and ripped longitudinally by pigs to expose their central core of food-rich mucilage. The starchy rhizomes of most of the tufted species are an added incentive to rooting.

With repeated baring of the floor and the continual fall of tall spreading trees now that the mutual protection of the closed canopy is gone, conditions are even less favourable to the seedlings normal to forest. On the other hand the aggressors—the ferns, the shrubby species of catholic tastes, and particularly *Microlaena,* are just as well suited as before, and now have the added advantage in their spread of an adequate supply of spores or seeds right at hand. Colonisation of the bare ground is hastened, too, by the vegetative spread of several species, notably *Blechnum discolor* (rhizomes), *Hemitelia* (adventitious buds) and *Microlaena*—this latter outpacing the rest and with them forming a complete ground-cover both in sunlight and shade. In many places the root-climbing *Freycinetia* persists, sprawling over the ground where light conditions are now so favourable for its growth and spread that it may cover several square metres at a stretch with its rather slender, brittle stems, topped by great arching tufts of yellow-green lanceolate leaves. *Paesia scaberula* now appears, becoming more or less abundant on drier, more insolated knobs, where it is often associated with a little *Histiopteris incisa* or *Gleichenia Cunninghamii,* and much greater quantities of *Acaena sanguisorbae,* its seeds carried by the various animals.

The end of Stage II. of change then shows (Pl. 51, fig. 1):

(1) CANOPY: The big trees have disappeared and the canopy is now formed by the survivors from the second layers (trees and shrubs from 5-6.5 m. high). The original species of the forest are still well represented—*Weinmannia racemosa, Olearia Cunninghamii, Suttonia salicina, Quintinia serrata, Ixerba brexioides, Coprosma grandifolia* and *Senecio Kirkii* occur at all altitudes. *Nothopanax Edgerleyi* (apparently less vulnerable than *Nothopanax Colensoi)* and *Melicytus ramiflorus* are still conspicuous in tawa, while *Phyllocladus glaucus* and *Griselinia littoralis* show similar staying-power in the kamahi.

The number of trees and the continuity of the canopy seem to depend almost entirely on wind. In a few shallow, sheltered valleys the crowns are still almost touching, but on exposed ridges the few severely pruned individuals that remain are widely separated and seem to owe something in their persistence to protective masses of such climbers as *Freycinetia Banksii, Metrosideros albiflora, M. hypericifolia, M. florida, M. scandens* or *Rubus schmidelioides,* which at least temporarily break the full force of the wind.

(2) MIDDLE LAYERS: *Hemitelia* is occasional to dominant, sometimes forming a new canopy about 6 feet above the ground between widely separated taller trees. *Drimys axillaris, Ascarina lucida, Brachyglottis repanda, Dracophyllum recurvatum* and *Hebe macrocarpa* form compact bushes of about the same height. *Freycinetia* occupies large areas.

(3) GROUND COVER: *Microlaena* is dominant. Associated with it are *Paesia, Histiopteris, Uncinia, Carex* and quantities of the various blechnums mentioned in Stage I. Together they form a mixed but fairly continuous cover in which logs and their half-dead epiphytes lie partly concealed.

STAGE III.

The inroads of pigs and goats continue. The fern population suffers as before, while *Freycinetia,* so important in Stage II., also succumbs. Its leaves are chewed and it is soon damaged by wind, but perhaps most devastating of all is the smashing of the brittle stems, thus exposing fresh portions of the interior of each clump.

Of the remaining trees kamahi persists longest, and though immune from direct animal attack, eventually it also is eliminated by wind action in all exposed parts. *Hemitelia,* hardy though it is, falls sooner or later before the same force.

Bare ground is once more available, but now in circumscribed areas hemmed in by *Microlaena. Paesia, Histiopteris* and/or *Acaena* may take charge temporarily, but they are soon encroached upon and swamped by the all-conquering grass.

Stage III. then is characterised by complete dominance of *Microlaena* as a ground-cover.

The ridges in particular show (a) total loss of canopy, (b) presence of scattered dying trees mainly derived from the middle layers of the forest. Ridges where this stage has been attained may be recognised from afar by the tawny mantle, which seems to have been thrown over them, its ragged fringes picking out the subsidiary spurs.

Only upon nearer inspection does one realise how many depressions, both large and small, are also dominated by *Microlaena.* As far as we can see the succession has proceeded on the same lines here in comparative shelter as it did in the open, the only differences in result being in the persistence of a more or less ragged canopy of relic trees. The presence of this canopy alone deprives *Microlaena* of the physiognomic dominance it enjoys in the open.

Everywhere in Stage III. stretches this expanse of *Microlaena,* its broad, rather harsh leaves standing rank on rank, softened in summer by the feathery daintiness of its slender inflorescences. Only on plunging waist-deep into this green, waving sea does one realise that it is not only in the trees of the park-like valleys that the forest leaves its mark. Ferns still occur, and everywhere the trailing *Rubus schmidelioides* gives a sharp reminder that it grows as vigorously through the grass as did its old stock stretching up into the tree-tops.

Even on those ridges that appear quite bare from a distance a few decadent trees still stand, their epiphytes now those of the old forest canopy (Pl. 52, fig. 1). Hidden tree-trunks are rotting everywhere, and where they project a little they bear a wind-bitten tangle of lianes.

A few of the smaller trees have shown themselves as adaptable as the lianes. Some, after falling, have grown sideways along the ground, and there, with their crowns partly protected by the grass, they thrive and flower. *Dracophyllum recurvatum, Knightia excelsa* and *Alseuosmia macrophylla* all behave in this way. *Dracophyllum* is perhaps outstanding for its staying-powers. It is characteristic of the windiest knolls, its great globular heads of shining green and crimson-stained leaves showing like gems in the pale matrix of *Microlaena* (Pl. 52, fig. 2). These plants are mainly survivors from the lower tiers, but many must have become established as seedlings well ahead of the general spread of the grass. Less abundant by far are *Drimys axillaris, Ascarina lucida, Hebe macrocarpa,* and *Brachyglottis repanda,* all in their young, bushy stages, and all showing signs of having been trimmed by animals. As yet these species offer no serious challenge to *Microlaena's* possession of ridge and hollow, though *Hebe* here and there forms small thickets, becoming more open with age.

Careful search shows that between the tufts of *Microlaena* little can establish itself. *Marchantia tabularis* Nees is not uncommon. Attenuated individuals of *Acaena sanguisorbae* var. and *Hypolepis tenuifolia* ramify amongst the grass, together with odd rejuvenated lianes of *Muehlenbeckia complexa*. *Juncus vaginatus* and a few species of *Carex*, also of tussocky life-form, may hold their own, but they show little sign of spreading. *Libertia ixioides* and *L. grandiflora* are locally abundant at lower levels, and surprisingly enough a few plants of *Gnaphalium keriense* were seen at about 750 m. On dry rock or clay uncolonised by *Microlaena*, *Metrosideros hypericifolia* and *Muehlenbeckia complexa* persist as low tight mats, and with *Danthonia semiannularis* var. *nigricians*, *Ranunculus hirtus*, *Oxalis corniculata* and *Gnaphalium luteo-album* form an open community. Exotics, conspicuously absent elsewhere, occur sparingly here, chief being *Festuca bromoides*, *Anthoxanthum odoratum*, and *Prunella vulgaris*. Only one plant of *Cnicus lanceolatus* was noted.

Cockayne (1928, p. 361) has pointed out that exotics do not gain entrance into primitive vegetation. It is even more remarkable that they are practically absent throughout a change from forest to grassland.

EXTENT ON MOUNTAIN.

Isolated plants of *Microlaena* are found on both ridge and stream-side almost to sea-level, but the species is aggressive only between 450 and 750 m. The succession described above is therefore co-extensive in altitudinal range with *Hemitelia Smithii* rather than with the species which is ultimately dominant. The upper limit is well defined (Pl. 52, fig. 1) and coincides with a somewhat abrupt change in structure in the original vegetation which here becomes either a wind-swept, mossy forest into the dark interior of which animals penetrate little, or a tight, low cover of species as aggressive as *Microlaena*, but better suited to the boggy conditions characteristic of the cloud-belt. *Astelia trinervia*, comparable to a grass in its tussocky growth-form, is here locally dominant, but is open to attack by pigs, which relish the mucilage so copiously exuded from the torn leaf-bases. Where *Astelia* has been cleaned out quite bare soil is left. Though this seems to be as yet too humus-rich and boggy for *Microlaena*, its seedlings have occasionally managed to establish themselves. It remains to be seen whether they will act as centres in the upward extension of the grassland formation.

The lower limit is less well marked and much more difficult to account for. It is a significant fact that it coincides with that of *Hemitelia*, which would thus appear to be essential to the initiation and progress of the succession. Below this level bracken *(Pteridium aquilinum)*, manuka *(Leptospermum scoparium* and *L. ericoides)* and occasionally *Aristotelia racemosa*, are aggressive in clearings. Though the first three species occur sporadically right up to the highest point on the ranges (but there also as aggressors) within the stated altitudinal limits they are not even locally abundant, and nowhere compete with *Microlaena* for the possession of fresh ground.

Though animals have been and still are free to range over the whole mountain, and no part can be considered strictly primitive, there are places, especially on the colder south-west slopes, where modification has been negligible and the original structure is preserved. Very steep faces, likewise, are practically untouched and where the soil is boggy a different succession is induced. With these exceptions, on every aspect of the mountain whether ridge, slope, or valley, a similar series of changes has been set in train. The stages described above are unavoidably somewhat schematic, but there is a remarkable uniformity in the whole succession, despite the very considerable floristic differences in the associations involved.

By far the greater part of the kamahi and tawa forest is similar in a general way to that described in Stage I. Whether this is in every case a stage in the same developmental succession towards grassland is not clear.

Stage II., more easily identifiable because of the definite establishment of *Microlaena,* occupies extensive areas mostly on flatter ridges and more gentle slopes, as well as always forming a broader or narrower band separating stages I. and III.

Stage III. is well represented in some half-dozen places. Many hectares on exposed ridges are practically devoid of trees, and the largest of these are of physiognomic importance in any view of the mountain. The total area held by any one stage can scarcely be estimated, but the greater part of the mountain within the altitudinal range of *Hemitelia* seems to be involved in one stage or other of the succession.

The **increase of ferns** after local or wholesale modification or destruction of rain-forest of this kind, e.g., after the fall of individual trees, landslips, or burning, may be considered normal, and often provides the shelter essential for the re-establishment of a community similar to, if not identical with the original. On Te Moehau the problem differs in that here the action of the destructive agents, the animals, is progressive, and especially detrimental to those very plants which represent the first stages in normal regeneration.

The new succession will depend on (1) propagules available, (2) ability of incoming species to establish themselves and persist under the particular conditions induced in the moribund community. As far as (1) is concerned the choice is wide, since animals, wind and water are efficient carriers on a slope where a vertical section from sea-level to 888 m. is not more than 5 km. in slant height, and where the plant-cover includes lowland pastures with exotic and indigenous grasses and weeds, manuka scrub, rain-forest, and the peculiar subalpine communities of the summit.

The phenomenal success of *Microlaena* indicates some peculiar fitness for colonising, either in structure or life-history, and this was sought in a more detailed study of the plant itself.

AUTECOLOGY.

SYSTEMATIC POSITION: *Microlaena avenacea,* sometimes called "Bush Rice Grass," is an endemic species of a genus which together with *Hierochloe* represents the tribe *Phalarideae* in New Zealand.

HABIT: The plant is tussocky, consisting of more or less closely packed tufts, reaching a height of 60-120 cms. The leaves arising round the bases of the tall unbranched culms are broad (c. 1.5 cms.), flat and harsh, with one prominent vein showing lighter than the rest of the blade, which is pale green or even glaucous. In exposed positions the tips of the leaves are often torn and discoloured, this raggedness being especially noticeable in winter. The sheaths are long and thin, and, as is indicated in the habit sketch of the plant, they give each tuft a narrow fan-like appearance. The blade may be either erect or drooping.

PHENOLOGY: On Te Moehau we look on the species as a midsummer flowerer. Though we know the range well in the summer months we have seen it at the height of its flowering season only in the late days of December and the early days of January. In the shade the season may be more protracted, as flowers are usually less advanced there than in the open.

INFLORESCENCE: The panicle is tall, the main axis slender, giving off compound hair-like branchlets at irregular intervals. The spikelets are conspicuously awned. They occur singly, greenish white in the open, or of a jade colour in the shade. However sparse they may appear on an individual, when seen in the mass they give such a generous feathery look as to transform the whole landscape.

The **fruits** soon mature, and owing to their method of attachment they are shed almost immediately, the sooner if they are exposed to wind, leaving the small, but conspicuous, glumes to whiten in the sun. The old panicles are eventually trampled down, or broken by wind, and typically by winter only the rather short more or less bleached leaves remain.

ROOT SYSTEM: The extent and importance of the root-system is shown by the following measurements of a fairly compact tussock taken from the top of a windy ridge (Stage III.).

Total height of flowering plant ..	58 cms.
Length of leaf	23 cms.
Depth of root-system	17 cms.
Spread of root-system	50 cms.

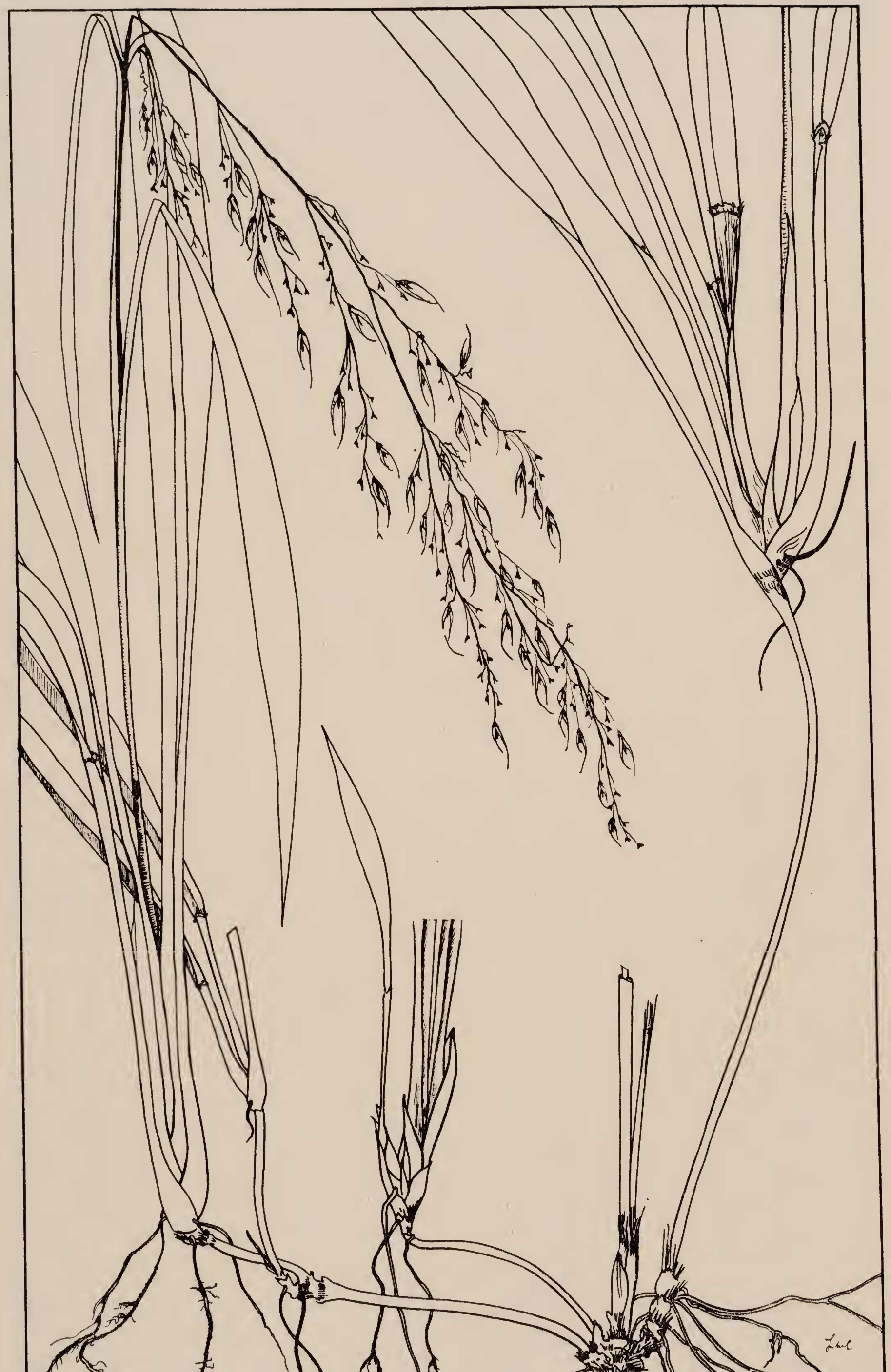
This depth of root-system is typical in that it represents ramifications throughout the whole of the shallow superficial soil. When sods of this size, or even much larger, full of the long, wiry, much-branched fibrous roots are occasionally upturned by pigs (in search of food) the more or less weathered greywacke subsoil is fully exposed.

Even in the seedling the root-system is well-developed. The young roots are slender, closely packed and of a pale straw colour. As the plant grows, more roots appear amongst the younger leaves of the elongating rhizome, as also on the offsets as they mature. Gradually the whole leafy portion of the tussock is thus lifted slightly, and the roots must plunge through an open accumulation of leaf-debris to reach the ground. This raising seems to be something of an advantage, especially where there is a tendency to local crowding of old tussocks and their litter.

VEGETATIVE SPREAD: Already in the seedling a vigorous vegetative growth is foreshadowed. The accompanying sketch (Text fig. 3) shows how early in development lateral shoots may appear. One bud has pushed into prominence after rupturing the sheath of the living leaf subtending it, while four more, hidden in the axils of the upper leaves, will soon appear. Such extravaginal shoots are always given off in rapid succession, so that a many-branched root-stock is developed (Text fig. 4). This lies above the soil level and is for long clothed by the sheath bases after the withering of the leaf-blades. Secondary roots develop freely. Normally under forest conditions the internodes remain short and the erect sheets are crowded together to form a rather compact tussock. Although a number of buds always so contribute to the formation of tussock, we have found that on Te Moehau in the open, many may, by elongation of one or more internodes, develop into stolons which are thrust far out radially from the parent plant. The stolons are stout, glabrous and often capable of removing the fans they bear 15-25 cms. from the older portions of the tussock. Each node roots and is firmly attached as it touches the ground, so that, except where tussocks are isolated, it is almost impossible to lift the whole root system intact.

The crowding of tussocks is not always overcome by the arching of the stolons. As is clearly shown in the sketch of a portion of an old clone (Text fig. 1), some of the nodes fail to reach the ground at all, simply through the bulk and lateral pressure of tall tufts hemming them in. In this state they grow on with undiminished vigour, either sprawling or almost erect, and often produce more or less normal sized panicles. Sturdy unbranched aerial roots frequently emerge from the unanchored nodes, but these are invariably short lived if the erect habit persists.

Death from old age, over-crowding, or even from rooting of pigs in search of food may follow for portions of the clone, and always individual tufts are being separated through the severing of the old stolons that link them. With such opening up the erect stolons are free to fall to the ground, where true anchoring and absorbing roots at last develop, instead of the earlier abortive aerial ones. This is the procedure where *Microlaena* is dominant and conditions fairly stable. In this way the exceptional vigour



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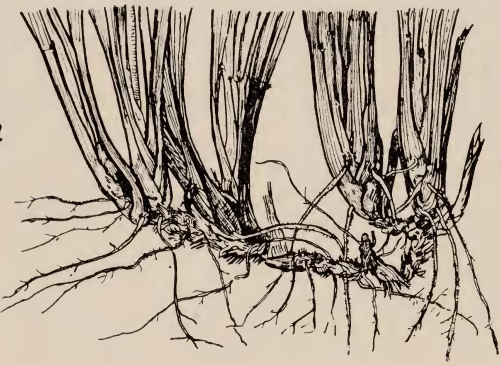

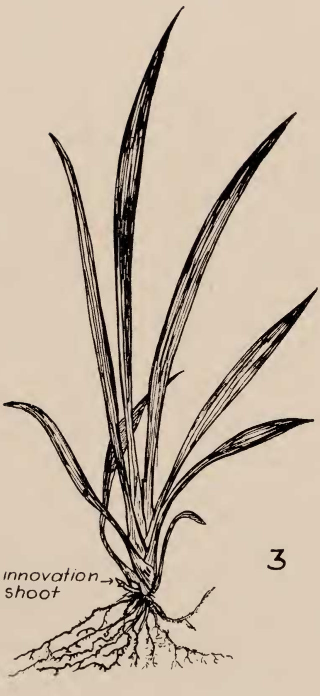

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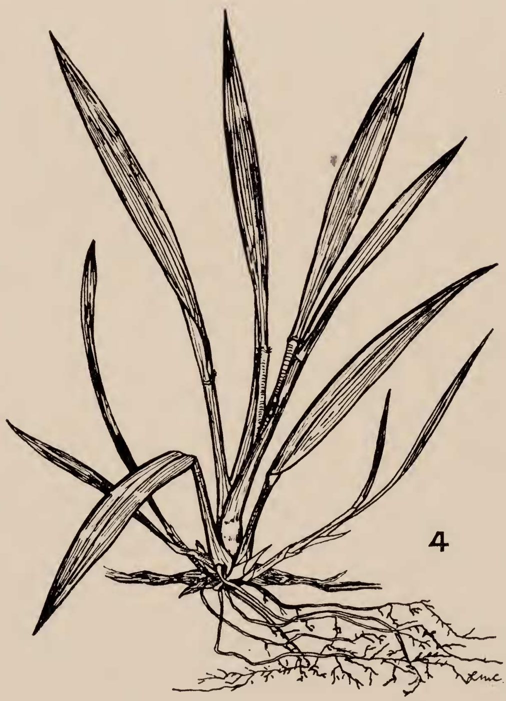

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Fig. 1 (opposite). Portion of flowering clone, showing long internodes and abortive aerial roots. Drawn from specimen collected on ridge.
Fig. 2. Root-stock from forest interior plant, showing short internodes.
Fig. 3. Seedling, showing first innovation shoot.
Fig. 4. Older seedling, showing three innovation shoots.

of the plant finds outlet in the exploitation of breaks in its own cover, and thus the even growth, so widespread on Te Moehau, is maintained. Naturally, where plenty of room is available for the plant to test its colonising powers, the stoloniferous habit stands it in splendid stead, and hence is of paramount importance in aggression as in maintenance of the community.

PART PLAYED BY SEEDS: The importance of the role of seeds in colonisation cannot, however, be under-estimated. They came somehow from the recesses of the original forest, and establishing, they have been the source of plants which must take up the struggle for supremacy from the beginning under totally new conditions. The progeny of the shade-loving tufts must be equally tolerant of light, of alternating drought and rain, and of greater temperature extremes than would obtain in the forest. Such broad tolerance is rare, but is demonstrated in the special success of *Microlaena* in widely differing situations, from the shadow and damp coolness of a stream-side forest station to the wind and heat of the exposed ridges. Here in the sun the big profusely-flowering tussocks produce infinitely more seed than ever appeared on the meagre culms in primitive forest.

SEED DISPERSAL: The individual fruits are relatively heavy and tend to fall immediately around the parent tuft, either into the maze of tangled stolons and drying leaves or, if it is isolated, towards its periphery and roughly as far removed from it as the outward sweep of the drooping branchlets of the inflorescence. The proof of the efficiency of this method of dispersal is seen in the local distribution of seedlings, which are always abundant against the outer margins of the tussocks. Thus in the spread of the indigenous induced community it may be said that *Microlaena* works steadily and rapidly along a vegetative front with a narrow outer fringe of seedlings.

Seed dispersal must often be more haphazard than this. Rain-wash and wind play their parts, but it is significant that we have seen neither seeds nor inflorescences blown through the air. The long awns tend to cling to any hairy surfaces, so it is probable that animals are rather important in dispersal over wide areas.

Viability of the seeds must be fairly high, as seedlings of all sizes were seen in January, usually the peak of the flowering season. Only once have we collected flowers that suggest that the dispersal of seeds might continue throughout the year. This was in May, that is, at the beginning of winter, but a solitary record such as this may have little bearing on the main problem of the source of seed supply.

HABITAT CONDITIONS: Seeds germinate freely on *Hemitelia* trunks up to a height of 90-120 cms., and on top of fallen logs. Flowers are often produced on epiphytic plants, showing that *Microlaena* is not restricted to any narrow limits in habitat conditions. Its failure to establish itself on very boggy places suggests a preference for rather well-drained situations, but its absence from the upper parts of landslips and from the very steep jagged rock outcrops that occur here and there on the ridges, proves that it is fairly sensitive to over-dryness of substratum.

As indicators of the range in the humidity of the atmosphere even where *Microlaena* has attained dominance, the epiphytes on the remaining trees on an exposed ridge might be compared with those in the shade of an adjacent park-like valley. On the ridge-top, on almost leafless trees, is *Astelia Solandri*, with its usual accompanying species (*Asplenium flaccidum, Dendrobium Cunninghamii, Earina autumnalis* and *Senecio Kirkii* especially noted). Partly dead masses of *Lepicolea scolopendra*, with more or less of the mosses *Macromitrium longipes, Dicnemon calycinum, Cladomnion ericoides* and lichens *Pannaria* sp. and *Sphaerophorus* sp., as well as cushions of *Dicranoloma Menziesii* and *Leptostomum inclinans*, together almost cover the trunks, while short tufts of *Usnea* sp. are quite common on terminal twigs. Particularly characteristic of this station, on trunks of tree ferns and decadent trees, is the coriaceous leaved fern *Polystichum adiantiforme*.

Polypodium diversifolium and *Madotheca Stangeri* (G.L. and N.), somewhat stunted where exposed, grow more luxuriantly on the trees of the valley. Here, from the spreading branches of sheltered *Melicytus ramiflorus* and *Fuchsia excorticata* and even from the nodes of the liane *Rhipogonum scandens* hangs the pendant moss *Weymouthia mollis*, its soft julaceous branches up to 30 cms. long and almost touching the tall plumes of the flowering grass below.

Grey and orange digitate *Sticta fragillima* abundant on rocks, and an occasional plant of the dendroid moss *Sciadocladus Menziesii* amongst the *Microlaena* tussocks are just as definitely relics of the original forest floor, and argue strongly against any radical change in habitat conditions.

OCCURRENCE OF MICROLAENA AVENACEA IN OTHER PARTS OF THE NEW ZEALAND BOTANICAL REGION.

With adequate means of seed dispersal, a very efficient system of vegetative reproduction, adaptability to a wide range of light, humidity and edaphic conditions, comparative immunity from animal attack, and a growth form suited to exclude competitors, *M. avenacea* would appear to be one of the best equipped species for aggression in forest, and might be expected to attain quite widespread dominance throughout its altitudinal and latitudinal range.

Buchanan (1880) says: "A tall, handsome grass, growing at low elevations. . . . Common in forest lands, and usually found there in small tussacs, which, by their confluence, often form large patches of a close, harsh sward, especially in the more open places."

According to Cheeseman (1925) it is abundant in forests throughout North, South and Stewart Islands, from sea level to 2,500 feet, and is "in forest, but not common," in Auckland Islands.

Cockayne (1928) records the species of podocarp-broad-leaved dicotylous lowland forest of both dry and wet ground, in the latter as a semi-obligate species of kahikatea (*Podocarpus dacrydioides*) semi-swamp forest. It is mentioned particularly in the description of this last community in the North-western Botanical District, where "As ground plants tall *Blechnum procerum, Astelia nervosa* var. *silvestris* and *Microlaena avenacea* are everywhere, and *Nertera dichondraefolia* and *N. depressa* are common. *Dicksonia squarrosa* is the dominant tree fern, and there is some *Hemitelia Smithii*." It is also included in the list of important members of one or more of the associations of montane and subalpine bog forest, of which the physiognomic trees are *Nothofagus*, cupressoid podocarps and *Libocedrus*.

Allan (1926) in a description of the podocarp forest on the flood plain of the Rangitata (E. Bot. Dist.) at 240 m., where *Podocarpus dacrydioides* is dominant and *P. spicatus* subdominant, and there is a dense undergrowth, states: "Floor plants are *Uncinia uncinata, Nertera dichondraefolia, Blechnum discolor, Microlaena avenacea, Hymenophyllum demissum,* but only where there is not an excess of water." Again, still treating of the same community, he says: "Where cattle enter milled forest open spaces increase and the forest becomes separated into clumps. Of special attraction to cattle are *Uncinia* spp., *Carex* spp., and, to a less extent *Microlaena avenacea*."

Our own work on Te Moehau has been supplemented by more general observations made during the last few years on diverse and widely separated examples of vegetation throughout the North Island.

Though nowhere, either in our notes or in the literature consulted, is there any reference to another example of such widespread induced dominance of *Microlaena avenacea* as we have described on Te Moehau, there is sufficient evidence of its comparative rarity in primitive forest and its tendency to increase as this is modified. Its phenomenal success in our area must depend on some quite local factor or combination of factors.

TAXONOMIC PROBLEM ARISING FROM STUDY OF INDIVIDUAL.

As has already been emphasised more than once, the stoloniferous habit is here of extreme importance. It is of interest, then, that the production of stolons is not mentioned in the Manual (Cheeseman, 1925) description of *M. avenacea,* leaving the inference that it must be a compact tussock of some kind. This overlooks the definite suggestion of extravaginal branching made by Raoul (1844) in the original description—"Radix repens more *Avenae pratensis*." On the other hand, *Microlaena Carsei,* according to Cheeseman (1915), the author of the species, is characterized by the vigour of its stolons. Our specimens certainly correspond with none of those of *M. Carsei* in the Cheeseman Herbarium, and by their habit they would appear to be excluded from *M. avenacea.* In our opinion the growth-form of this latter species is inadequately treated in current descriptions, which, however, cover the case of the crowded tussock habit sufficiently well. This does not preclude the possibility of the development of stolons, especially under changed habitat conditions, so we have no hesitation in claiming that ours is an epharmonic form of the forest interior grass.

By the same token it is yet possible that the rare and consequently little known *M. Carsei* may be either a jordanon or some habitat form of *M. avenacea.* Reference to Carse's full and interesting series of specimens in the Herbarium of the Museum shows that all were collected in open places in kauri forest, giving more than a hint that they also belong to more or less modified forest. The status of *M. Carsei,* however, and particularly that of *M. avenacea,* are problems for the taxonomist. All we can do is to draw attention to the undoubtedly powerful influence of environmental factors on life form.

It may be of interest to note that though *M. stipoides,* a much smaller pasture grass, occurs in abundance in the lowlands and up to a height of about 300 m. on Te Moehau, where in small ridge openings it is associated with *M. avenacea,* we have seen no indication that the two species cross. *M. polynoda* was recorded for Coromandel by Adams (1888), but we have not seen it here. It appears, then, that the possibility of hybridism is very remote.

ECONOMIC ASPECT.

Of *M. avenacea* Buchanan (1880) says: "This grass is greedily eaten by cattle during winter, when it then becomes valuable in supplementing the more nutritious leaf food from certain trees, such as Karaka *(Corynocarpus laevigata),* Mahoe *(Melicytus ramiflorus),* and several others which form their chief food during that season in many places. This species can hardly be recommended for cultivation, as in open country it would very probably become harsher and less succulent; but settlers living in the neighbourhood of forests would be repaid the trouble of collecting seed and sowing it among the trees, and by that means increasing the amount of winter food for their cattle."

Adams (1888) and Allan (1926) also mention its being eaten by cattle.

We have been told, but have no means of verifying the statement, that while cattle remained on Te Moehau they grazed on *M. avenacea* and that, since this check has been removed, the grass has shown a marked increase in rate of spread.

Certainly our observations show that no animals now on the mountain feed to any appreciable extent on the grass. Fortunately, the "bush" is not now so often expected to provide winter feed for cattle, the farmers realising that in this area at least the loss of numbers in the unfenced upper parts of the mountain more than balances any profit gained from those that do return to the pastures in spring.

As a fodder plant, therefore, the grass is of little value. The community, nevertheless, is of very considerable economic importance in that it provides a close cover on ridges and slopes, where, with destruction of forest, landslips and floods become a real danger to the farms below. While its work in holding soil and lessening run-off amply justifies its existence, it must not be forgotten that the very presence of this grassland is an indication of a sorry state of affairs. It bears testimony to the fact that hordes of destructive animals are being maintained on land owned and controlled by the State. Not only are these useless as revenue producers, but they are a constant menace, destroying the natural balance between the vegetation and its environmental factors. *Microlaena* temporarily saves the situation, but there are places where it is powerless. Even if, ultimately, the boggy summit parts of the mountain, the very steep faces, and the rocky portions of landslips are colonised, in the interval between the opening up of these and the re-establishment of ground-cover there is grave danger.

Interesting though it would be to watch this great experiment to the end, to find to what extent the forest would ultimately be ousted and its place usurped by grassland, we know that it is of more permanent value to advocate the extermination of animals from this easily isolated area and a more strict interpretation of the name State Forest Reserve even now applied to the greater part of Te Moehau.

SUMMARY.

1. An account is given of the development of a community dominated by *Microlaena avenacea* depending upon the progressive action of introduced animals in rain forest.

2. The composition and structure of the original forest, the ecological conditions to which it is subject, and the succession itself, are briefly described. The main changes are (a) opening of forest, (b) increase of ferns and *Microlaena,* (c) destruction of ferns and dominance of *Microlaena.* The succession is strictly limited in altitudinal range.

3. Reasons for the success of *Microlaena* are sought in the study of its autecology.

4. Records of the occurrence of the species in other parts of New Zealand are briefly reviewed, its taxonomic status discussed, and the protectional value of the indigenous-induced community stressed.

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Fig. 1. Typical opening in Stage II., showing *Microlaena* in full flower, abundance of *Hemitelia* and shrubs surviving from tawa forest.

Fig. 2. *Microlaena* stretching through park-like area. Dead trunks and dying tree-ferns in foreground.

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Fig. 1. Stage III. at 700 m., showing well-marked upper limit on left. Dark patches in foreground are *Muehlenbeckia* and *Paesia*.

Fig. 2. Typical short-trunked *Dracophyllum recurvatum* persisting in Stage III.